

Observations on Australian Solemyidae

by R.G.B. Reid and
D.G. Brand

Department of Biology, University of Victoria,
Victoria, B.C. V8W 2Y2 Canada

ABSTRACT

Two species of Australian Solemyidae are examined. Gross structure, the condition of the gut, the histological organization of the gills, and the presence of intracellular gill bacteria are noted. *Solemya velesiana* (Iredale) is a small, intertidal protobranch with large ctenidia, and a functional gut. The species oxidizes sulphide and intracellular gill symbionts appear to contribute to its economy. Museum specimens of a species assigned to *Solemya australis* Lamarck also have large ctenidia with intracellular bacteria. The gut of this species is much reduced and the organism thus must be more dependent on sulphide-oxidizing symbiosis.

INTRODUCTION

For more than a century the living Solemyidae have been objects of curiosity because of their much reduced alimentary tracts, a condition first noted by Pelseneer in 1891. The species discussed by Yonge (1939), *Solemya velum*, and *S. togata*, are small deposit feeders, and their gut reduction roused no suspicions. However, Owen (1961) pointed out that in the relatively large New Zealand species, *S. parkinsoni*, the minute gut could not possibly provide an adequate digestive process and he suggested that extra-organismic digestion might occur in the mantle cavity. A more striking problem was raised by the discovery of a gutless species *S. reidi* (Reid and Bernard, 1980). Coincidentally, the gutless Pogonophora of the Galapagos Rift hydrothermal vent communities were discovered to possess symbiotic bacteria that could use the energy of sulphide oxidation to fix carbon dioxide, and similar symbionts were then discovered in the ctenidia of *S. reidi* and *S. velum* (Cavanaugh et al., 1981; Felbeck et al., 1981; Felbeck, 1983; Cavanaugh, 1983). It may be inferred that other gutless Solemyidae such as *S. borealis* and *S. solen*, as well as gutless members of the solemyoid family Nucinelidae, are largely dependent on the sulphide-oxidizing symbiosis, although the uptake of dissolved organic molecules is a potential nutrient supplement in environments where there is much organic debris (Reid, 1987; Shepard, 1986). The symbiosis has also been discovered in Solemyidae that retain the gut, and two questions therefore arise: to what extent does normal alimentation satisfy the nutritional requirements of such species, and how universal is the occurrence of the symbiosis in the Solemyidae? Reid and Brand (1986) argue that the sulphide-oxidizing symbiosis was the major driving force of the evolution of the solemyoid Protobranchia, and although this argument would not be greatly vitiated by the discovery of a

species that lacked the symbiosis, more comprehensive evidence on the symbiosis and its morphological correlations is desirable. For this purpose we examine here two species of Australian Solemyidae that possess alimentary tracts.

MATERIAL AND METHODS

Specimens of *Solemya velesiana* (Iredale) were collected at Pioneer Bay, Orpheus Island, Queensland, in the mid-tidal area of the mud flats behind the fringing reef. Some were examined by dissecting microscope at the laboratory of James Cook University on Orpheus Island. Particles of alumina, carborundum, latex and sephadex (in the size range of 10 μm -120 μm) were used to detect ciliary movement of particles. The particles found in natural pseudofaeces were also measured. Others were fixed in Bouin's fixative for subsequent embedding in JB4 plastic. Some specimens were fixed in glutaraldehyde for embedding in epon for transmission electron microscopy, and some glutaraldehyde-fixed material was dried and gold coated for scanning electron microscopy. Details concerning fixation and staining are provided by Reid and Brand (1986). A large specimen of *Solemya australis* Lamarck from King George Sound was examined for the morphology of the mantle cavity, and partially dissected to study the gut. Other specimens that had been collected intertidally in sand near Perth, Western Australia and had been fixed in formalin, and preserved in alcohol, were embedded in JB4 polymethacrylate for serial sectioning, or epon-embedded and sectioned for transmission electron microscopy. One specimen was studied by scanning electron microscopy.

Serial sections of specimens of *S. velesiana* and *S. cf. australis* (see below) were stained with periodic acid Schiff stain (PAS), which indicates the presence of polysaccharides, and also stains the symbiotic bacteria. Alcian blue was used to detect acid mucopolysaccharide, with eosin as the counterstain. Control sections treated with diastase (α -amylase) provided information on the distribution of glycogen.

Note on the taxonomy of *Solemya* in Western Australia

At the present time only *Solemya australis* is recorded from the southern part of Western Australia (Cotton, 1961; Roberts and Wells, 1980). There is, however a possibility that as many as three species may have been identified as *S. australis*. Slack-Smith (pers. comm.) has raised a question concerning the identity of the most commonly collected intertidal *Solemya* which always appears to be in the less than 1cm size range of *S. velesiana* and *S. terraereginae* (Iredale), the latter being a tropical species that we did not obtain. Among the larger individuals held by the Western Australian Museum we noted some variability in shell shape and in the relative sizes of the gills; but we do not possess sufficient material to clarify this issue. We have opted for the conservative tactic of describing three individuals, of intermediate sizes, which were all consistent in relative gill size, labial palp form, gut size, and in having an anteriorly expanded shell, and of calling these *Solemya cf. australis*, noting here that this will probably be subject to subsequent taxonomic revision. A specimen of this type has been lodged with the Western Australian Museum.

RESULTS

Distribution

Solemya velesiana occurs intertidally; its type locality being Green Island, Queensland. The bivalve inhabits well-defined, V-shaped burrows that are lined with a thin layer of mucus. The burrows are easily detected while digging since they are marked with an orange-brown halo of ferrous iron which is probably due to the oxidation of iron sulphide in the reducing environment when exposed to the oxygen drawn through the burrows by ventilation currents (Dando et al, 1985). The average depth of the burrows is 15cm and the animals were most commonly found at depths between 5 and 10cm, with the anterior ends uppermost. The sediment below 5cm does not have a strong sulphide odour, and by the Dando olfactory test appeared to have a sulphide content of no more than 0.1 μm , i.e. barely detectable to a human nose of average chemosensitivity (Dando et al, 1985). Depletion of sediment-bound sulphide may require frequent re-burrowing. The species was not found in the high sulphide environment of the upper intertidal mangrove,

nor in cleaner sand in the mid-tidal of other parts of Pioneer Bay. Specimens that had been recently dug up and placed in clean sea water were observed to swim by jetting water through the exhalant opening, in the manner of *S. velum* and *S. reidi* (Reid, 1980).

Solemya australis Lamarck, the type species of *Solemya*, is widely distributed in southern Australia (Cotton, 1961). Its preferred environment is not known. Since it is known to be an active swimmer (like other Solemyidae), this species may choose favourable environments. *S. australis* is found in the benthos of its type locality in King George Sound and in the adjacent, shallow Oyster Harbour in the Albany area of Western Australia (Roberts and Wells, 1980). Specimens of *Solemya* cf. *australis* in the collection of the Western Australian Museum have been found intertidally in sand in W. Australia.

Pallial Functional Morphology

Solemya velesiana has large aspidobranchiate, or bipectinate ctenidia, characteristic of the Solemyidae. (Fig 1A, 2A). They are dark brown in colour, which may be due to the presence of haemoglobin and bacteria (Felbeck, 1983; Doeller and Colacino, 1987). The frontal cilia of the distal margins of the lamellae beat ventrally, and particles ranging in size from 10 to 300 μm accumulate to form mucus-bound pseudofaeces which are voided through the exhalant opening. The mucus appears to be produced largely by the hypobranchial gland in the suprabranchial chamber. There is no evidence of particle-sorting by the gills nor any indication of the anterior movement of particles recorded by Yonge (1939) for *S. togata*. The cilia of the gills therefore appear to have only a cleansing function. The labial palps are relatively large, with a basal expansion. As in other Solemyidae there are no sorting ridges and grooves, and the palps may be the homologues of the palp proboscides of the nuculoid Protobranchia (Yonge, 1939). There is no evidence in either of the species under investigation of the separate palp pouch homologues that occur in *S. reidi* (Reid, 1980). In section the palps are crescentic, and the convex and concave surfaces are ciliated. The cilia of the outer convex surfaces beat towards the palp margins, and those of the concave inner surfaces beat towards the base of the palps, whence a narrow ciliated tract carries particles to the mouth. The palps can be extended anteriorly through the pedal gape, but we were unable to observe the natural feeding posture as it might occur in the animal's burrow.

The ctenidia of *Solemya* cf. *australis* are also relatively large but the labial palps are small when compared to those of *S. velesiana* (Fig. 1B and 2B). A distinct food groove runs from the base of each palp towards the mouth.

Histology and Ultrastructure of Ctenidia

The gill lamellae in the two species under investigation have the same structure as has been reported for *S. reidi* (Reid 1980; Powell and Somero, 1985). The crescentic lamellae are attached by a short septum to the visceral mass (Fig. 3). Each lamella has a double supporting rod of chitin near the ventral margin (Fig. 3 and 4A). The cells distal to the chitinous rod are ciliated and possess numerous mitochondria. Proximal to the chitinous rod is a large blood vessel which communicates with the extensive blood spaces between the two epithelial layers of the lamellae. The proximal lamellar tissue consists of two cell types. The narrow intercalary cells contain mitochondria, and have microvillar distal borders that partially overlap the surfaces of the adjacent bacteriocytes (Fig. 4B). The bacteriocytes, which alternate with the intercalary cells, contain numerous bacteria (Fig. 4B). The bacteria stain strongly with PAS and this staining persists in diastase-treated sections which have lost their glycogen granules. This staining therefore gives a preliminary indication of the presence of bacteria, both in freshly fixed tissue and in museum material. At the EM level the presence of the bacteria can be confirmed e.g. in *S. velesiana* (Fig. 4B) and in museum specimens of *S. cf. australis* (Fig. 4C). High magnification of the museum material confirms that the granular residue of the bacteriocytes does consist of bacteria, with characteristic cells walls and chromosomal content, although the cell membranes of the bacteriocytes have largely disintegrated, and mitochondria are no longer recognizable. In the preparations from this species, the alternating arrangement of bacteriocytes and intercalary cells can be vaguely discerned. Note that the nuclei of the intercalary cells are usually evident, but that because of the large size of the bacteriocytes a given section will miss some of their nuclei (Fig. 4B).



Figure 1.

- A. Scanning electron micrograph of ventral surfaces of *Solemya velesiana*. Shell is removed; foot is anterior.
- B. Composite scanning electron micrograph of ventral surfaces *Solemya* cf. *australis*. Shell is removed; foot is anterior.

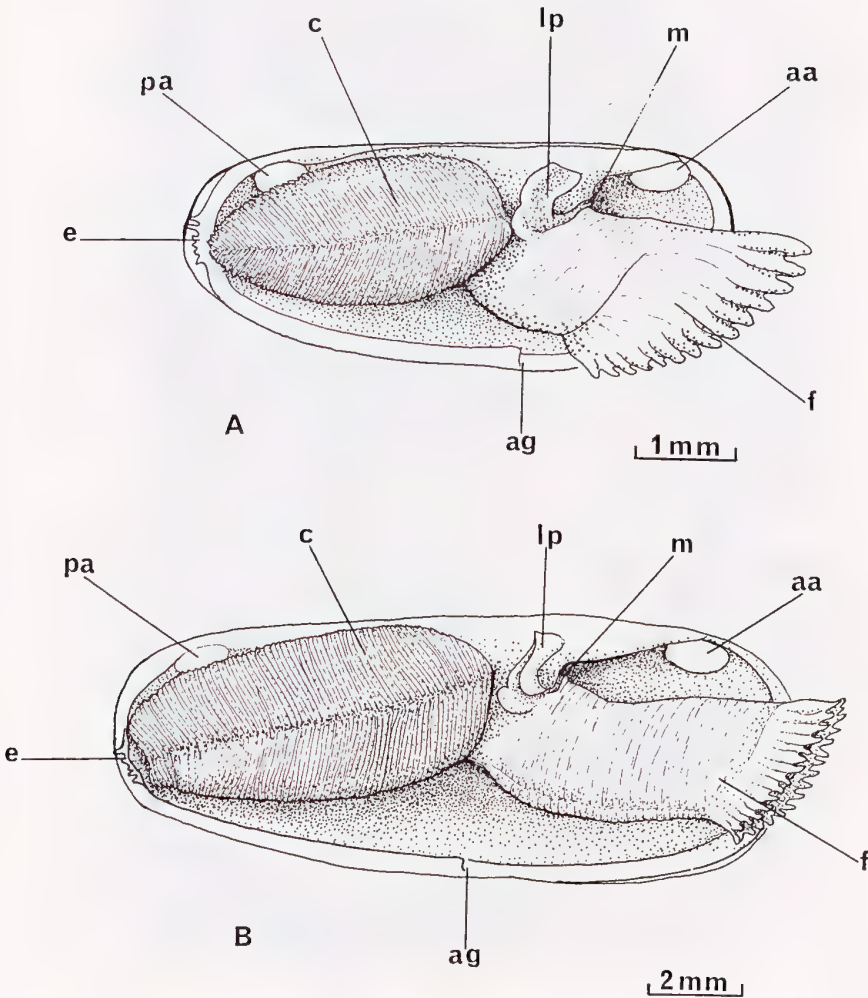


Figure 2.

A. Diagram of right side of *Solemya velesiana*; shell removed.

B. Diagram of right side of *Solemya cf. australis*; shell removed.

Abbreviations: aa — anterior adductor muscle; ag — posterior limit of anterior gape; c — ctenidium; e — exhalant siphon; f — foot; lp — labial palp; m — position of mouth; pa — posterior adductor muscle.

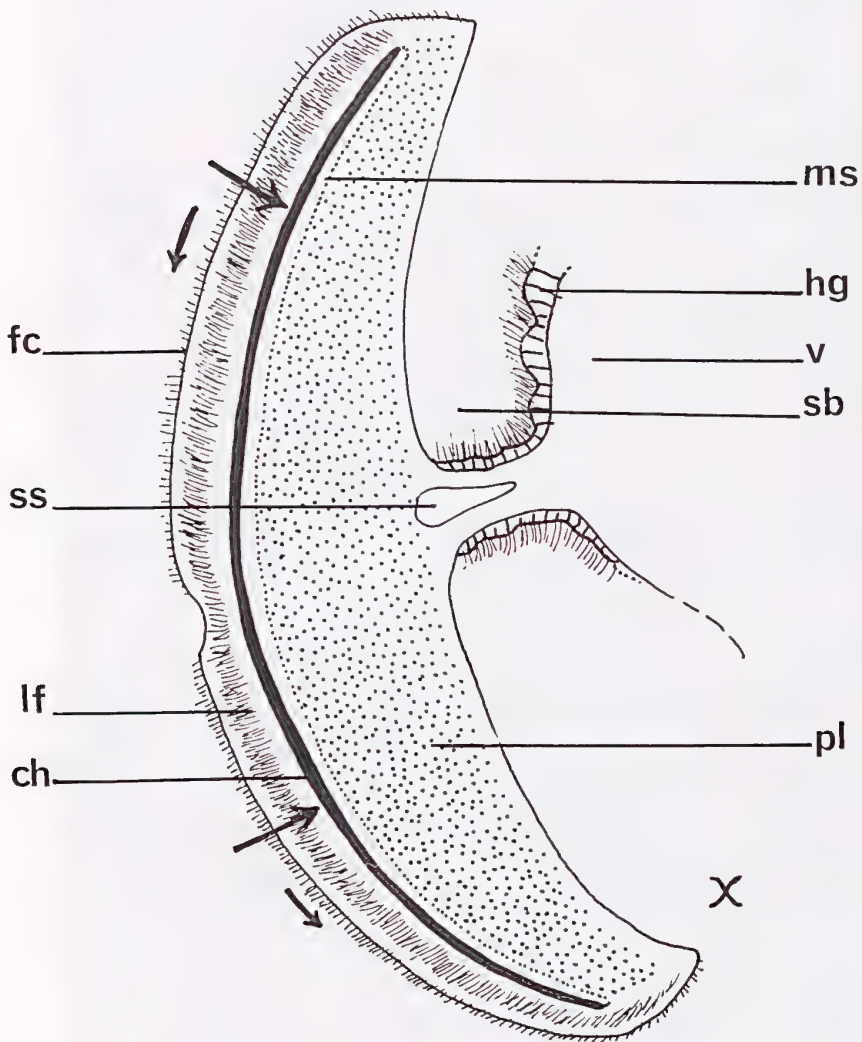


Figure 3.

Stylised diagram of *Solemya* ctenidial lamella. Pseudofaeces collect at X.

Abbreviations: ch — chitinous supporting rod; fc — frontal cilia; hg — hypobranchial gland; lf — latero-frontal cilia; ms — position of marginal blood sinus; pl — proximal region of lamella, made up of bacteriocytes and intercalary cells; s — septum; sb — suprabranchial chamber; ss — septal blood sinus.

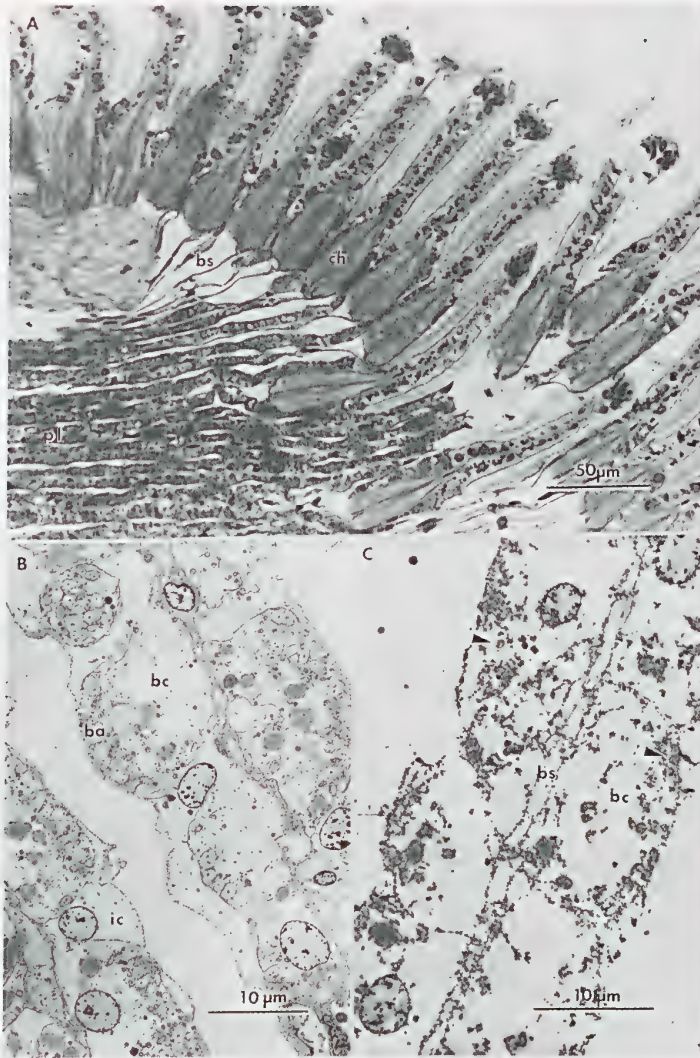


Figure 4.

A. Light micrograph of a transverse section of the gill lamellae of *Solemya velesiana*
 B. Transmission electron micrograph of gill lamellae of *Solemya velesiana*
 C. Transmission electron micrograph of formalin-fixed, alcohol-stored museum material of *Solemya* cf. *australis*. Arrows indicate bodies that can be determined to be bacteria at higher magnification.

Abbreviations: ba — bacteria; bc — bacteriocyte; bs — blood sinus; ch — chitinous supporting rod; ic — intercalary cell; pl — proximal region of lamella made up of bacteriocytes and intercalary cells.

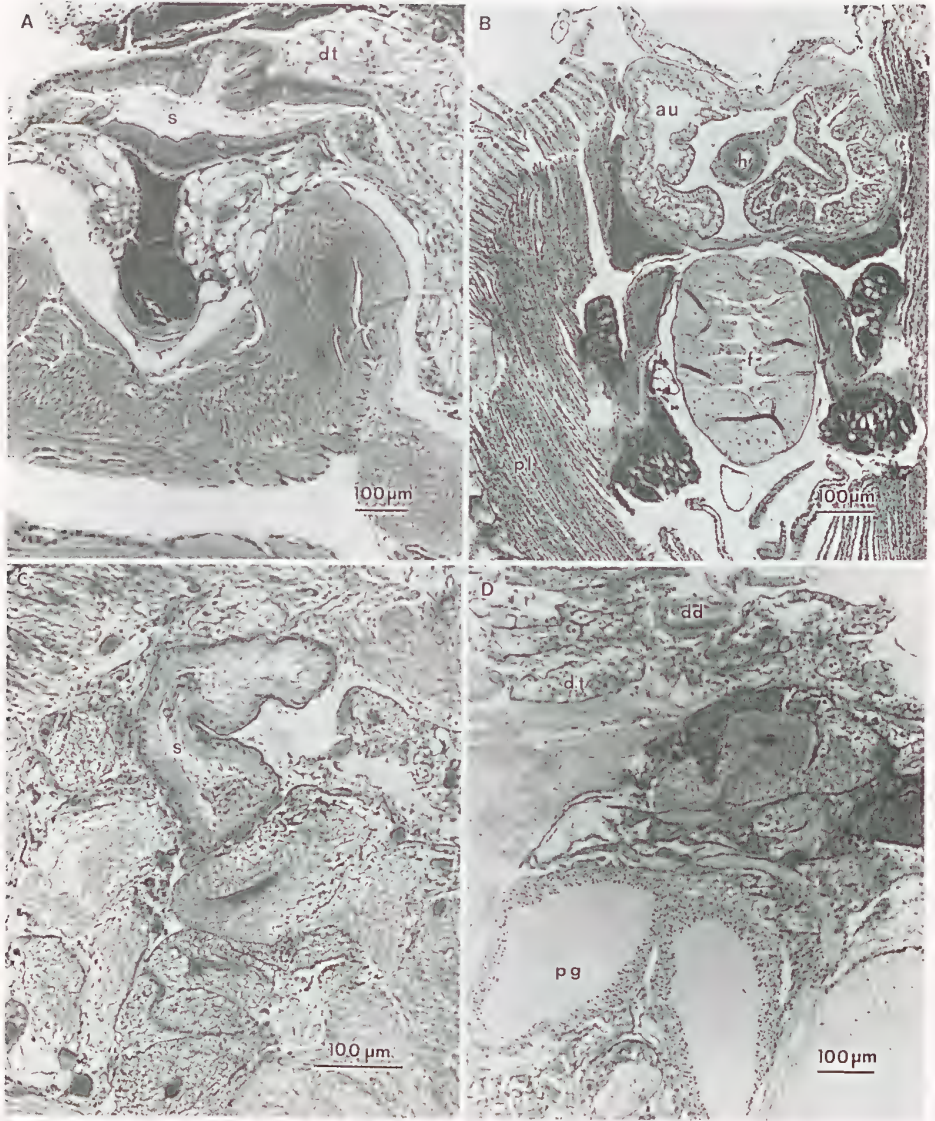


Figure 5.

JB4 (polymethacrylate) transverse sections

A. Gastric region of *Solemya vesesiana*

B. Cardiac region of *Solemya vesesiana*

C. Gastric region of *S. cf. australis*

D. Region of digestive diverticula and pedal ganglia of *S. cf. australis*

Abbreviations: au — auricle; dd — diverticular duct; dt — digestive tubule; f — foot; h — hind gut; pg — pedal ganglia; pl — proximal region of gill lamellae, containing bacteriocytes and intercalary cells; s — stomach.

Alimentary Tract

The oesophagus is short in both species. The stomachs differ in relative sizes and complexity. In transverse sections the stomach of a 1cm specimen of *S. velesiana* reaches a maximum of 1mm in diameter (Fig. 5A). The stomach of a 2.5cm specimen of *S. cf. australis* did not exceed 1mm (Fig. 5C). In each species the digestive diverticula consisted of a few small acini (Fig. 5A and D). The diverticular epithelia of *S. velesiana* have large lipid droplets that appear as vacuoles in material that has been dehydrated in alcohol (Fig. 5A). In both species the mid gut is narrow, short and relatively unconvoluted. Particles found in the guts of *S. velesiana* and *S. cf. australis* were in the size range of 5 - 30 μm .

DISCUSSION

Solemya velesiana, and *S. cf. australis* both possess reduced alimentary tracts. This is more common than the gutless condition of *S. reidi*, *S. borealis* and *S. solen* (Reid, 1986). In *S. reidi* there is never a complete, functioning gut; separate rectal, gastric and oesophageal rudiments present in the late pericalymma larvae disintegrate at metamorphosis (Gustafson, 1985). Where present, the gut of most *Solemya* species would not appear adequate to nutritionally support these relatively large, active bivalves. As Owen (1961) remarked concerning the large species *S. parkinsoni* the stomach is barely large enough to contain a single diatom of respectable dimensions. Some indication of the importance of the alimentary tract may be derived from the proportions of the gut and gills relative to the whole organism. On these grounds, the digestive processes of the gut of *S. velesiana* would appear to be a significant source of nutriment. The presence of relatively large labial palps and the lipid depots in the digestive diverticula support this conclusion. Furthermore this species has sources of detrital food from the mangrove and the fringing reefs. The gills are also large in this species, indicating that the sulphide-oxidizing symbiosis is also important.

In *Solemya cf. australis* the gills are relatively large and the gut more reduced than that of *S. velesiana*. Specimens held by the Western Australian Museum are recorded as having been collected intertidally in sand in eelgrass beds. Fisher and Hand (1984) have observed that eelgrass roots may provide symbiotic Lucinidae with a source of photosynthetic oxygen, which along with sulphide is necessary for symbiotic metabolism. Reid and Brand (1986) review the different routes of uptake and internal partitioning of oxygen and sulphide in all bivalves in which the sulphide-oxidizing symbiosis has been found. Powell and Somero (1986) have discovered that in *Solemya reidi* the mitochondria of the host bivalve initiate the sulphide oxidation and produce ATP from the initial oxidation. The role of the symbiotic bacteria would then be the provision of essential amino acids and fatty acids that the bivalves cannot synthesize for themselves. This is also likely to hold in Solemyidae with alimentary tracts which cannot adequately contribute to nutrition. According to our unpublished observations *S. reidi* rapidly absorbs dissolved amino acids and sugars from the environment when these are available. Shepard (1986) has demonstrated that these dissolved organic molecules (DOM) are available at significant levels in environments where organic debris is being decomposed by free-living anaerobic bacteria. This may help to sustain the juveniles of *S. reidi* until the gills and their symbionts have developed adequately.

In those species of *Solemya* that retain guts, the alimentary tract may be particularly important for normal nutrition during the crucial stage between metamorphosis and gill expansion. In the adults the gut may provide an additional route for sulphide absorption (Reid and Brand, 1986).

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